

1 Personal information about danger trumps social information from avian alarm calls

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## Abstract

Information about predators can mean the difference between life and death, but prey face the challenge of integrating personal information about predators with social information from the alarm calls of others. This challenge might even affect the structure of interspecific information networks: species vary in response to alarm calls, potentially because different foraging ecologies constrain the acquisition of personal information. However, the hypothesis that constrained personal information explains a greater response to alarm calls has not been experimentally tested. We used a within-species test to compare the antipredator responses of New Holland honeyeaters, *Phylidonyris novaehollandiae*, during contrasting foraging behaviour. Compared to perched birds, which hawk for insects and have a broad view, those foraging on flowers were slower to spot gliding model predators, showing that foraging behaviour can affect predator detection. Furthermore, nectar-foraging birds were more likely to flee to alarm call playbacks. Birds also assessed social information relevance: more distant calls, and those from another species, prompted fewer flights and slower reaction times. Overall, birds made flexible decisions about danger by integrating personal and social information, while weighing information relevance. These findings support the idea that a strategic balance of personal and social information could affect community function.

Keywords: alarm call, information use, social information, anti-predator

## INTRODUCTION

Information about predators is critical for survival [1, 2]. Broadly, there are two types of information available to an individual: a) personal information, which is gained by an individual observing a predator or other threat directly, and b) social information, which comes from the signals or cues provided by other individuals that have detected the threat [3]. Alarm calls, which warn others of the presence of a threat, are a rapidly transmitted and widespread source of social information [4, 5]. When these two types of information concur, this can result in greater certainty and efficiency in the decisions an individual makes [6, 7]. However, when the available social information conflicts with prior personal information, individuals need to assess the relative value of the two types of information. The outcome of this decision can depend on the quality of the information, such as its reliability or relevance, [8, 9] and how easy the information is to acquire [10]. For instance, when personal detection of predators is impeded by visual obstructions [11], information from others may become especially valuable. The integration of personal and social information may be particularly important for decision-making in the context of predator avoidance, where the stakes are very high.

Foraging ecology may affect individuals' ability to gather personal information and, consequently, their reliance on social information [12, 13]. For example, in mixed-species foraging flocks, species that feed high in the canopy and hawk for insects respond less to alarm calls than species that glean insects from the foliage or ground [14, 15]. This difference in reliance on social information has been attributed to the possibility that flycatching species, which scan for prey from a perch, are better at detecting predators than gleaning species. While there is observational evidence to suggest that perching species may spot predators sooner [16], causal relationships cannot be inferred from such observations alone and this assumption has not been tested experimentally.

Reliance on social information may be determined by differences in the relevance of alarm calls, in addition to the ability to spot predators. Many vertebrates eavesdrop on the alarm signals of other

species in their environment, gaining access to additional social information [17]. However, alarm calls of some species may be perceived as less relevant than others because they are given by heterospecifics with overlapping but not identical predators, reducing receiver responsiveness [9, 18]. For example, great black-backed gulls, *Larus marinus*, are much larger than herring gulls, *L. argentatus*, leading to differences in predator vulnerability. The larger black-backed gulls consequently show a reduced response to herring gull alarm calls compared to conspecific calls, whereas the smaller gull responds similarly to both species' calls [19]. Interspecific variation in response to alarm calls can thus be driven by differences in the perceived relevance of the information.

Studying within-species differences in the use of personal and social information about predators can potentially illuminate the mechanisms driving between-species differences in avian communities. Comparisons across species can be difficult to interpret because species differ in many ways, such as in their vulnerability to predators [20], visual acuity [21] or escape tactics [22]. Furthermore, as heterospecific alarm calls differ in their relevance to different species [9, 19, 23], it is important to consider both the amount of personal information available and the relevance of the social information to understand species' responses to alarm calls. Even the attributes of individual receivers within a species, like their plumage colouration or age, can influence how they use social information [24, 25]. Therefore, an alternative approach to testing the hypotheses for interspecific patterns of eavesdropping is to assess differences in information use within individuals in a species that has multiple foraging methods.

Here we make use of natural variation in the foraging strategies of New Holland honeyeaters, *Phylidonyris novaehollandiae*, to examine how wild birds use both personal and social information about danger. Individual honeyeaters use multiple foraging techniques, feeding on nectar by probing flowers and hawking insects from exposed perches [26, 27]. These foraging strategies may result in different amounts of personal information: individual birds are likely to have a clearer view of their surroundings when perched, so should have access to more personal information than when nectar-foraging, because

of a restricted view when probing flowers [28, 29]. Honeyeater foraging behaviour thus mirrors the ecological differences between flycatching and gleaning species in mixed-species foraging flocks [14, 15]. As such, it is possible to experimentally test the assumption that foraging behaviours affect the acquisition of personal information and to assess how the availability of personal information shapes the use of social information. The results can provide insights into the causes of interspecific differences in information use.

We predicted that individuals would have less personal information about danger when nectar-foraging, and should therefore be more responsive to social information, than when perched. To test whether nectar-feeding birds are in fact less able to spot predators, we presented focal individuals with gliding model predators when they were either perched or nectar-foraging. We then carried out two playback experiments to investigate how the foraging strategy of the focal bird affected its response to alarm calls. In each experiment, we also varied the relevance of the social information presented to the birds, presenting them with less relevant information in the form of more distant alarm calls and alarm calls from another species, the white-browed scrubwren (*Sericornis frontalis*).

## METHODS

### *Study site and species*

We studied New Holland honeyeaters and white-browed scrubwrens between June 2014 and February 2017 in the Australian National Botanic Gardens in Canberra, Australia. Both species are resident in the Gardens, a 40 ha area of natural and planted vegetation, and accustomed to the presence of people.

New Holland honeyeaters are small (20 g), pair-breeding passerines that probe flowers for nectar and hawk insects from the air [26]. White-browed scrubwrens are smaller (14 g), cooperatively breeding passerines that glean insects from the ground [30]. Both species are vulnerable to avian predators in the Botanic Gardens, such as collared sparrowhawks, *Accipiter cirrhocephalus*, which feed on small birds, and

102 pied currawongs, *Strepera graculina*, which are primarily nest predators but will opportunistically target  
103 small adult birds [31, 32].

104 Both honeyeaters and scrubwrens produce multi-element aerial alarm calls to flying threats, that  
105 prompt listeners to flee for cover [9, 33]. A honeyeater alarm call consists of repeated elements that have  
106 a peak frequency of around 3.5 kHz, a monotonic decline in frequency and an amplitude of about 70 dB  
107 at 6 m (85.5 dB at 1 m assuming geometric spreading) [9] (Fig 1a). Scrubwren aerial alarm calls are  
108 acoustically distinct from honeyeater alarm calls with a peak frequency of 7 kHz, a dual-band structure  
109 with rapid frequency modulation and an amplitude of about 58 dB at 6m (73.5 dB at 1 m assuming  
110 geometric spreading) [33, 34] (Fig. 1b).

111 Further methodological details of the experiments described below are provided in the electronic  
112 supplementary material.

### 113 ***Model presentation experiment***

114 To test whether different foraging strategies affect an individual's ability to detect predators and  
115 therefore gain personal information, we carried out model presentations to 20 New Holland honeyeaters,  
116 presenting each bird with a model predator once when it was perched and once when it was foraging  
117 upon flowers. Two exemplars of life-sized gliding models, painted to resemble an adult or juvenile collared  
118 sparrowhawk, were used to simulate an airborne threat [35]. Presentations to the same bird were  
119 separated by a minimum of 30 minutes (mean  $\pm$  SE: 100 mins  $\pm$  18), and individual birds received the same  
120 model exemplar in both presentations. The models were presented by a thrower standing about 15 m  
121 from the focal bird with minimal obstructions between them.

122 Two Panasonic HC-V770M camcorders were used to get exact timing of bird responses to  
123 predator models. One camcorder recorded the model's flight, while the second recorded the focal bird's  
124 response. The thrower was kept blind to whether the focal bird was perched or nectar-feeding. The  
125 thrower waited near a feeding site used often by the focal bird, and threw the model hawk in a pre-

determined direction when prompted by the observer. The observer prompted the thrower by playing back the word “throw” through a speaker placed at least 7 m from the focal bird. We used playbacks to ensure that the prompts were standardized and would not contain any unintended cues revealing the behaviour of the focal bird. These playbacks were also used to synchronise the videos from each camera. Using the video recordings, we determined whether the bird detected the model, the time it took for the bird to detect the model, and whether the bird fled to cover after detecting the model. Detection of the model was defined behaviourally as a rapid head turn that oriented the bill towards the model, or a rapid vertical extension of the neck when oriented towards the model, resulting in a head-up movement [21, 36, 37]. The time to detection was measured as the time from when the model left the thrower’s hands to when the bird showed one of the above behaviours. Detection was followed by freezing, sneaking, visually tracking the model, alarm calling, fleeing or any combination thereof.

### ***Playback experiments***

#### *Recordings of alarm calls*

Natural honeyeater alarm calls were recorded between June 2014 and August 2015 using Marantz PMD670 and PMD661 MKII digital recorders, sampling at 44.1 kHz at 16 bits, and a Sennheiser ME66 shotgun microphone. The birds were followed at a distance of 10 – 20 m. Crimson rosella, *Platycercus elegans*, contact bell calls were recorded as control playbacks (Fig. 1c). White-browed scrubwren alarm calls were prompted with a gliding model predator.

#### *General playback methods*

We conducted two playback experiments on 20 colour-banded New Holland honeyeaters to investigate the effects of foraging strategy and alarm call relevance on social information use. All playbacks were prepared in Raven Pro 1.4 (Fig 1). Playbacks were broadcast from a Roland R-09HR via a custom-made amplifier and a Peerless tweeter speaker attached to the experimenter’s waist. Responses

to playbacks were recorded using a Panasonic HC-V520 camcorder supported by Wizmount CU2 pack over the experimenter's shoulder, filming at 25 frames per second at 640x360 pixels.

The experiments tested whether the foraging strategy of the birds affected their response to alarm calls of varying relevance. Both experiments followed the same design. Each bird received a unique set of exemplars of all alarm and control playbacks (details below), and all birds received each playback set twice over a period of two days: once when they were nectar-foraging on the edge of cover and once when they were perched at least 0.5 m from cover. Playback order was randomized within a block design to minimize order effects. Playbacks were carried out from a distance of 7 – 10 m, a minimum of 5 minutes apart (mean  $\pm$  SE: 34 mins  $\pm$  3) and during which no alarm calls were produced or predators were nearby. If a playback presentation was interrupted by a disturbance such as a loud noise, alarm call or arrival of a predator, it was repeated at the end of the day.

The video recordings of the responses were analysed using Adobe Premiere Pro and QuickTime. The scorer was blinded to the playback treatment by removing the soundtrack after noting the frame number of the onset of the playback, renaming the video files and randomizing their order prior to analysis. We scored whether the birds responded to the playbacks and how they responded. The immediate response of the bird was first scored as: 0 (no response), or 1 (all other responses). For birds that did respond, we then categorized their responses as 1 (immediate flight to cover), or 0 (all other responses). By scoring only immediate flight to cover, the normal response to multi-element alarm calls, we ensured that the birds were not gathering additional personal information about danger by scanning first but instead were relying entirely on the social information from the alarm playbacks. We also measured the latency to respond as the time from the onset of the playback to the time when the bird initiated a response.

#### *Experiment 1: Effect of alarm call distance*



In order to test the effects of foraging strategy and call distance on social information use, birds were presented with 3 playbacks: (1) a 7-element alarm call at natural amplitude of 70 dB at 6 m, (2) a degraded version of the same 7-element call at an amplitude of 57.5 dB at 6 m, and (3) a crimson rosella bell call at an amplitude of 70 dB at 6 m as a neutral control. Calls were degraded by broadcasting them through the undergrowth and re-recording them from a distance of 25 m [38]. As birds pay attention to both signal amplitude and degradation when assessing the distance to a sound source [38, 39], we included both cues to increase the likelihood that the honeyeaters would perceive the two alarm treatments as originating at different distances. Nearby alarm calls should indicate an immediate threat and prompt flight to cover, whereas distant alarm calls may be less relevant and result in information-seeking behaviour, such as scanning. We predicted that birds would respond more strongly to the playbacks when a) they were nectar-foraging, and b) the playbacks simulated a closer caller.

#### *Experiment 2: Effect of alarm calling species*

To investigate the effects of foraging strategy and calling species on social information use, birds were presented with 4 playbacks: (1) a 7-element New Holland honeyeater aerial alarm call at natural amplitude of 70 dB at 6 m, (2) the same 7-element honeyeater call at a reduced amplitude of 57.5 dB at 6 m, (3) a 4-element white-browed scrubwren aerial alarm call at natural amplitude of 57.5 dB at 6 m, and (4) a crimson rosella bell call at an amplitude of 70 dB at 6 m as a neutral control. As the natural amplitude of honeyeater alarm calls is louder than that of scrubwren alarms, the reduced amplitude honeyeater treatment was included to assess the relative importance of amplitude and call type. Scrubwren alarm calls may not be perceived as always relevant from the perspective of the New Holland honeyeaters. An observational study found that around 20% of scrubwren alarms were given to non-predators, whereas the honeyeaters never called to non-predators [9]. We predicted that birds would respond more strongly to the playbacks a) when they were nectar-foraging, and b) of honeyeater alarm calls compared to scrubwren alarm calls.

## ***Statistical Analysis***

All statistical analyses were carried out in R version 3.4.1 [40]. Bias-reduced generalised linear models (BRGLMs) were constructed with binomial error distributions and logit link functions, using the `brglm()` function of the `brglm` package [41, 42]. Generalised linear mixed-effects models (GLMMs) were constructed with binomial error distributions and logit link functions, using the `glmer()` function of the `lme4` package [43]. We constructed the linear mixed-effects models (LMMs) with normal error distributions and identity link functions, using the `lmer()` function of the `lme4` package. The identity of the focal individual was included as a random effect in all mixed-effects models. We carried out pair-wise comparisons using the `glht()` function of the `multcomp` package [44]. In all cases, the full model with all terms of interest was fitted before likelihood ratio tests were used to identify significant fixed effects by removing them individually from the model and assessing the change in deviance.

### ***Model presentation experiment***

Whether the birds responded to the predator model in any way and whether they fled to the predator model were entered as the response variables in generalised linear mixed effects models. To look at the latency to detect the model, we used a linear mixed-effect model. The fixed effects for all models were the position of the bird, the presentation order, and the distance from which the model was presented.

### ***Playback experiments***

To look at whether the birds responded in any way to the playbacks, we used a bias-reduced generalised linear model to account for complete separation in some categories, with the birds' response entered as the binary response variable. As birds never fled to the controls, these were excluded from the analysis of fleeing response. The fleeing response was entered as the binary response variable in a generalised linear mixed-effects model. The latency to respond underwent a logarithmic transformation to improve fit before being entered as the response variable into a linear mixed effects model. For all

220 models, the playback type, position of the bird, the day, and playback order within the day were entered  
221 as fixed effects. The identity of the focal individual was included as a fixed effect in the bias-reduced  
222 generalised linear model, because such models cannot incorporate random effects. For the two mixed-  
223 effects models, focal bird identity was entered as a random effect instead to account for the repeated  
224 measures design.

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## RESULTS

### *Model presentations*

Nectar-feeding birds reacted more slowly to the model predator than did perched birds, but when they did react, they were more likely to flee to cover. Although the bird's foraging strategy did not affect the probability of detecting a model (GLMM:  $\chi^2 = 0.19$ ,  $df = 1$ ,  $p = 0.66$ ; Table S1), nectar-foraging birds took over 220 ms longer to detect the model than perched birds (LMM:  $\chi^2 = 4.55$ ,  $df = 1$ ,  $p = 0.03$ ; Table S1; Fig. 2a), which shows that nectar-foraging birds had restricted personal information. Furthermore, nectar-foraging birds were almost three times as likely to flee to cover than perched birds, implying that they perceived a higher degree of risk because they had less information (GLMM:  $\chi^2 = 6.09$ ,  $df = 1$ ,  $p = 0.01$ ; Table S1; Fig. 2b).

### *Experiment 1: Effect of alarm call distance*

Honeyeaters responded more strongly to playbacks when they were foraging on nectar and when the social information was more relevant. Birds were more than twice as likely to show a response to alarm playbacks than to controls (BRGLM:  $\chi^2 = 64.14$ ,  $df = 2$ ,  $p < 0.001$ ; Tukey's test:  $p < 0.00$ ; Table S2). Over 95% of birds responded, at least by scanning, to alarm playbacks, irrespective of either the call distance (Tukey's test:  $z = 0.54$ ,  $p = 0.085$ ) or the foraging strategy of the bird (BRGLM:  $\chi^2 = 0.38$ ,  $df = 1$ ,  $p = 0.54$ ; Table S2; Fig. 3a). However, following playbacks of alarm calls, the honeyeaters were more than twice as likely to flee into cover when they were nectar-foraging than when they were perched (GLMM:  $\chi^2 = 15.06$ ,  $df = 1$ ,  $p < 0.001$ ; Table S2; Fig. 3b), with a similar latency to respond (LMM:  $\chi^2 = 0.013$ ,  $df = 1$ ,  $p = 0.91$ ; Table S2). Birds fled to cover only half as often in response to the alarm playbacks that simulated a more distant caller (GLMM:  $\chi^2 = 8.17$ ,  $df = 1$ ,  $p = 0.004$ ; Table S2; Fig. 3b).

### *Experiment 2: Effect of alarm calling species*

Consistent with the previous experiment, individuals were more likely to flee to cover to playbacks of alarm calls when nectar-feeding than when perched (GLMM:  $\chi^2 = 22.72$ ,  $df = 1$ ,  $p < 0.001$ ; Table S3).

Once again, more birds responded, at least by scanning, to alarm playbacks compared to control playbacks (BRGLM:  $\chi^2 = 65.98$ ,  $df = 3$ ,  $p < 0.001$ ; Tukey's test: all  $p < 0.001$ ; Table S3; Fig. 4a). Regardless of the calling species (Tukey's test: all alarm comparisons  $p > 0.08$ ) or the foraging strategy of the bird (BRGLM:  $\chi^2 = 0.30$ ,  $df = 1$ ,  $p = 0.59$ ; Table S3), around 90% of birds responded to alarm playbacks, showing that the social information is assessed rather than ignored. By contrast, only about 35% of birds showed any response to controls. Birds were slower to react to playbacks when perched, taking about 40 ms longer than when they were foraging (LMM:  $\chi^2 = 6.78$ ,  $df = 1$ ,  $p = 0.009$ ; Table S3; Fig. 4b).

Birds were more likely to flee, and responded faster, to conspecific than heterospecific alarms. As predicted, birds fled more than twice as frequently to conspecific alarm calls than to the scrubwren alarm calls when both were played at their natural amplitude (GLMM:  $\chi^2 = 13.55$ ,  $df = 2$ ,  $p = 0.001$ ; Tukey's test:  $z = -2.94$ ,  $p = 0.009$ ; Table S3; Fig. 4c). But playback amplitude affected the probability of fleeing, as the honeyeaters were also more than twice as likely to flee to conspecific alarms at their natural amplitude of 70 dB than to the same calls at a reduced amplitude of 57.5 dB (Tukey's test:  $z = 2.91$ ,  $p = 0.01$ ). In contrast, the latency to respond to playbacks was influenced only by the species presented (LMM:  $\chi^2 = 23.68$ ,  $df = 3$ ,  $p < 0.001$ ; Table S3; Fig. 4b). The honeyeaters responded similarly quickly to honeyeater alarms played at their natural amplitude or at a reduced amplitude (Tukey's test:  $z = -0.56$ ,  $p = 0.94$ ), which suggests that lower amplitude playbacks were not harder to detect. Despite this, the birds took around 100 ms longer to respond to the scrubwren alarms than to the honeyeater alarms at both natural (Tukey's test:  $z = 4.14$ ,  $p < 0.001$ ) and reduced amplitude (Tukey's test:  $z = 3.44$ ,  $p = 0.003$ ).

## DISCUSSION

Individuals with reduced personal information about danger were more reliant on the social information provided by conspecific and heterospecific alarm calls. Birds took significantly longer to spot the model predator when nectar-foraging than when perched. Consistent with this, birds were more likely to flee to cover if the alarm playbacks were presented when they were foraging with a restricted view of their environments than when they were perched. The relevance of the social information also affected responsiveness, with heterospecific alarm calls and playbacks simulating a more distant caller prompting fewer individuals to flee. These results demonstrate that foraging strategies can affect the amount of personal information individuals have about predators, which in turn impacts their reliance on alarm calls, and may thus shape patterns of heterospecific eavesdropping in communities.

### *Amount of personal information*

The results of the model presentation experiment support the idea that perched birds can detect predators more easily than nectar-foraging birds. Individuals that were perched reacted on average 220 ms sooner to the model predator than when nectar-foraging. A hunting raptor could gain up to 5 m in that time [45, 46], making it a meaningful difference in reaction time. Moreover, it is likely to be an underestimation of the differences in detection between perched and nectar-foraging birds, as the models were always presented on the same side of the bush as the side on which the birds were nectar-feeding. In reality, predators could approach from the opposite side to a nectar-feeding bird, reducing the ease of detection and likely resulting in slower reaction times for nectar-feeding birds. The greater delay to react in nectar-foraging birds is consistent with previous work on captive birds that found that individuals take longer to detect oncoming models when their heads are down [21, 47], as well as an observational study on mixed species flocks in which perched birds were quicker than foraging birds to produce alarm calls in response to predators [16].

Individuals might be expected to adopt a strategy of better-safe-than-sorry when presented with conflicting information about danger, as the costs of ignoring information could be very high. However, across all experiments, birds rarely fled to cover when perched. As such, it seems that, when presented with model predators, individuals with a clearer view of the predator could more accurately assess the degree of danger they are in, while in the playback experiments, birds that could see there was no predator nearby devalued the social information provided by alarm calls. The pattern of social information use found here across different feeding strategies in individual honeyeaters is consistent with research on species differences in reliance on heterospecific alarm calls, where species that spend more time foraging on substrates or low in the canopy tend to respond more strongly to alarm calls than species that hawk for insects from perches. This suggests that variation in access to personal information across species, as a result of different foraging ecologies, could be the mechanism driving patterns of eavesdropping and species' associations in communities [12, 13, 15].

While the response of the honeyeaters in this study is consistent with foraging birds having reduced visual information, it is possible that constraints on attention could also play a role. When birds are engaged in cognitively demanding foraging tasks, they are slower to detect peripheral targets or approaching predators, suggesting that foraging birds may be constrained by the limited cognitive load available to them [48, 49]. However, this idea is inconsistent with the finding that honeyeaters reacted as quickly, or even faster, to alarm calls when feeding as they did when perched, although it might explain why nectar-foraging honeyeaters took longer to spot model predators. Nonetheless, both limited attention and visual obstruction in nectar-foraging birds could result in individuals suffering from reduced personal information about predators.

Honeyeaters rarely ignored the alarm calls entirely. Birds that did not immediately flee almost always engaged in other anti-predator behaviours, such as scanning or fleeing after a period of scanning. Given that neither the foraging strategy of the bird nor the relevance of the alarm calls affected the

likelihood of the honeyeaters responding to the calls, it suggests that the differences in fleeing behaviour are not due to an inability to hear some playbacks. As perched birds can see further, they may therefore have enough time to gather additional personal information before deciding whether to flee. Furthermore, foraging birds may be targeted by predators more often than vigilant individuals [50, 51], which could explain why in one experiment birds responded more rapidly to playbacks when they were nectar-foraging. As a result of their greater vulnerability, foraging birds could be primed for danger and able to react more quickly. Together, these results suggest that birds integrate both sources of information, which enables them to avoid potentially paying a fatal price while reducing energetically expensive flights.

#### *Relevance of social information*

The relevance of the social information also played an important role in determining its use. The honeyeaters responded more strongly to alarm calls that simulated a nearby caller than to calls that had been degraded and attenuated to represent a more distant caller. Individuals calling from further away may potentially be a less relevant source of information or could provide less urgent information, as the threat is also likely to be more distant, resulting in receivers seeking further information about the threat, rather than fleeing immediately into cover [38]. As the honeyeaters showed similarly reduced responsiveness to conspecific calls played back at a reduced amplitude without degradation, it is possible that birds use amplitude alone as a proxy for distance or that quieter calls signal lower urgency [38, 39].

Eavesdropping on heterospecific alarm calls can provide a valuable source of information, as it means there are more individuals looking out for danger, some of which may be better at detecting predators than others [17]. However, honeyeaters were less likely to flee to scrubwren alarm calls than to conspecific calls when both were played at their natural amplitudes of 57.5 dB and 70 dB at 6 m, respectively. Several studies have reported lower response rates to heterospecific alarm calls, likely because heterospecifics are not vulnerable to the same suite of predators, rendering some of their alarm



calls irrelevant to eavesdroppers [17, 18]. Not only did honeyeaters flee less frequently to heterospecific alarm calls, they also responded more slowly to scrubwren alarms. Weaker signals are associated with slower reaction times [52, 53], but the quieter amplitude of the scrubwren alarms is not sufficient to explain the difference as the birds responded similarly swiftly to conspecific calls played at both natural and reduced amplitude. It is probable that honeyeaters have to learn to recognize the acoustically dissimilar scrubwren alarm calls [17, 54, 55], which could lead to a longer neural processing time for the learnt calls [56, 57]. Previous work suggests that birds are able to discriminate more quickly between conspecific calls than between heterospecific calls [58], and in humans, *Homo sapiens*, individuals react more slowly to words in their non-native language [59]. Longer processing times of acoustically dissimilar alarm calls could affect the flow of information among species. Together, these results suggest that there can be both clear and subtle advantages to using conspecific information.

#### *Conclusion*

This study demonstrates that birds can make flexible decisions in the context of danger by differentially valuing information from distinct sources, balancing their own personal observations against information from others. These results support previous work showing that not all information on danger is equal – both the type of information [10, 60, 61] and its quality [9, 62, 63] can have significant effects on how it is weighed, even during very rapid flee responses. By incorporating information from multiple sources, birds can mitigate the costs of fleeing to false, or irrelevant, alarm calls while avoiding fatal predator encounters when they are most vulnerable. The study provides experimental evidence that foraging techniques can constrain personal information about danger and can lead to increased reliance on social information, supporting the idea that the relationship between foraging ecology and information use could play an important role in structuring interspecific patterns of eavesdropping in avian communities.

**Ethics**

This work was carried out under permits from the Australian National University Ethics Committee.

**Data accessibility**

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.25s5j4g>

**Authors' contributions**

J.R.M. and R.D.M. conceived the study; J.R.M. and C.P.R. carried out the fieldwork; and all authors contributed to the writing.

**Competing interests**

We have no competing interests.

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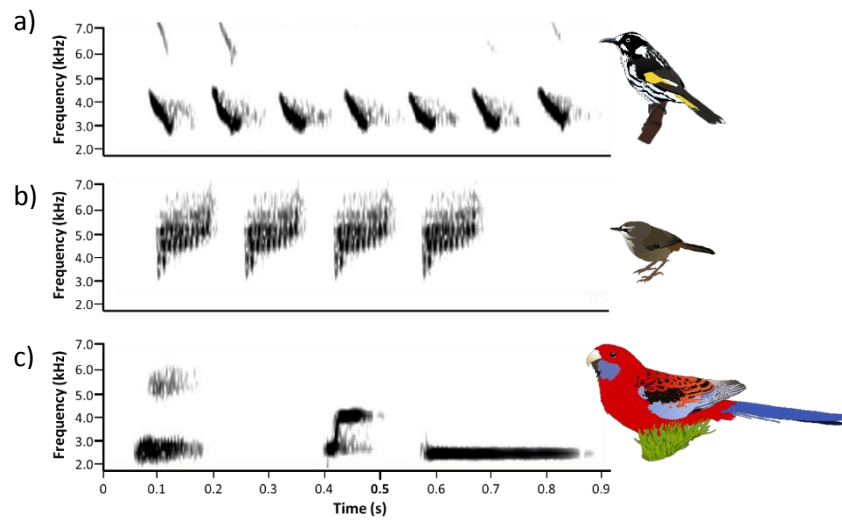
## Figure captions

**Figure 1.** Spectrograms showing examples of a) New Holland honeyeater alarm, b) white-browed scrubwren alarm, and c) crimson rosella contact call. Spectrograms were produced in Raven 1.5 using a Hann window function with a 256 sample size, a temporal grid resolution of 2.9 ms with an overlap of 50% and a frequency grid resolution of 172 Hz. Images created in Adobe Photoshop CC, approximately to scale.

**Figure 2.** Response of birds to model presentations according to foraging strategy: Honeyeaters were a) quicker to respond to models when perched than when nectar-foraging ( $p = 0.03$ ; Table S1a; 1 frame = 20 ms), and b) more likely to flee to models when nectar-foraging than when perched ( $p = 0.01$ ; Table S1b). Columns represent raw means, and bars are standard errors;  $N = 20$  birds. Images created in Adobe Photoshop CC, showing a honeyeater foraging on *Banksia* sp. inflorescence or perched.

**Figure 3.** Experiment 1 – Effect of alarm call distance: Honeyeaters were more likely to a) respond in any way to alarm playbacks than to controls ( $p < 0.001$ ; Table S2a), and b) flee to playbacks simulating nearer, rather than further, callers ( $p = 0.004$ ) and when nectar-foraging than when perched ( $p < 0.001$ ; Table S2b). Columns represent raw means, and bars are standard errors;  $N = 20$  birds. Image information given in Figure 2.

**Figure 4.** Experiment 2 – Effect of alarm calling species: Honeyeaters a) were more likely to respond in any way to alarm playbacks than to controls ( $p < 0.001$ ; Table S3a), b) responded more rapidly to playbacks from conspecifics than from heterospecifics ( $p < 0.001$ ) and when nectar-foraging than when perched ( $p = 0.009$ ; Table S3c; 1 frame = 40ms), and c) were more likely to flee to honeyeater alarms at natural amplitude than to reduced-amplitude honeyeater alarms or natural-amplitude scrubwren alarms ( $p = 0.001$ ) and when nectar-foraging than when perched ( $p < 0.001$ ; Table S3b). SW-57.5dB = scrubwren alarm at 57.5 dB; NH-57.5dB = honeyeater alarm at 57.5 dB; NH-70dB = honeyeater alarm at 70 dB. Amplitudes are at 6 m from the speaker. Columns represent raw means, and bars are standard errors;  $N = 20$  birds. Image information given in Figure 2.

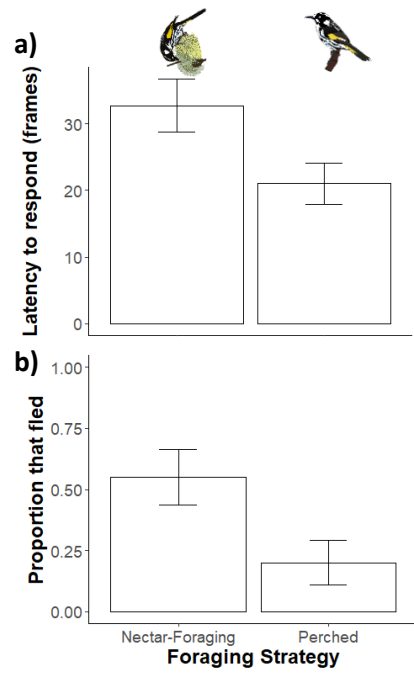


**Figure 1.**



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**Figure 2.**

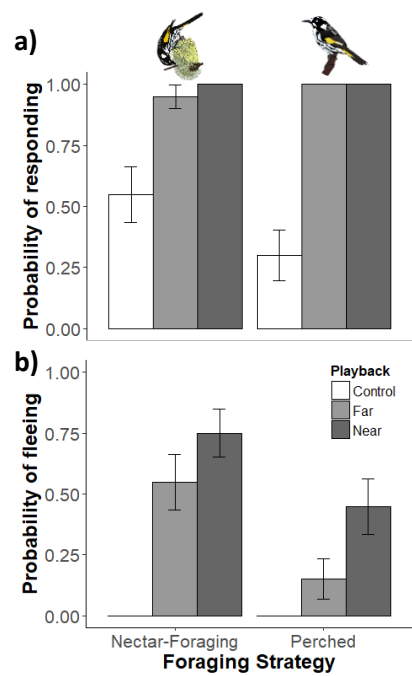


Figure 3.

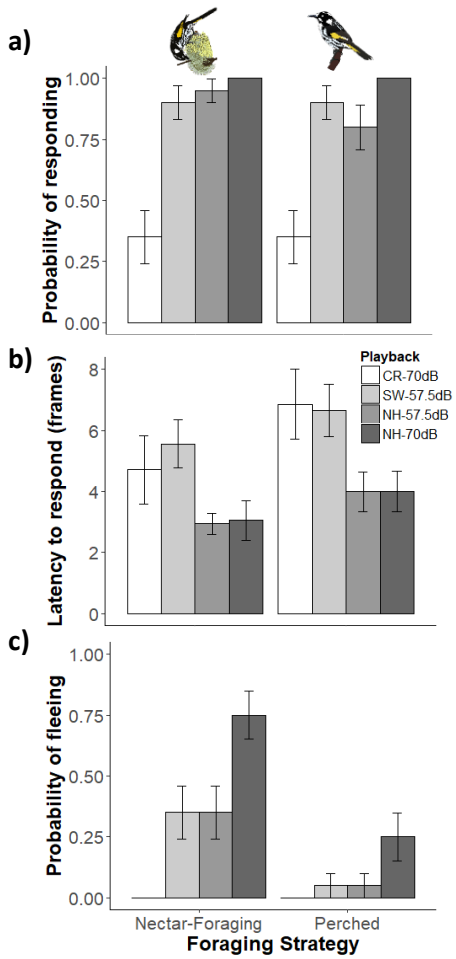


Figure 4.